

ECOLOGICAL ECONOMICS OF FORAGING AMONG COEVOLVING ANIMALS AND PLANTS

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The papers presented in this symposium focus on the reciprocity between plants and their associated fauna. Some studies approach plant-pollinator interactions at generic or familial levels and treat distributions over broad expanses of evolutionary time (*e.g.* Beattie, Gentry, and Ramírez). Others examine selected habitats and community interactions on ecological time scales (*e.g.* Ayensu, Heithaus, Macior, and Strong). Generally, one goal is to document specific boundaries which allow definition of floral resources relative to specific faunal consumers. I want to relate some of these new findings to recent research on consumer "switching" between alternative food resources.

Early studies of pollination did not consider the gathering of pollen and nectar as generalized modes of foraging, but Robertson (1899) did recognize the similarity when he stated, "The relations of the host-bees to the flowers from which they get pollen are quite analogous to the relations of parasites to their hosts, of phytophagous insects to their food plants, or of predaceous insects to the insects upon which they feed" Pollination ecologists currently use terminologies and classifications for describing pollinator behavior which are different from those applied to predatory behavior, but there is a continued recognition of the general similarity between these distinct types of foraging. For instance, a pollinator which visits a single plant species for pollen and nectar is termed "monotropic," and Faegri and Pijl (1971) comment, similar to Robertson, that "its relation to the blossom is more or less on the lines of a host-parasite relationship." Michener (1954) has also noted that bees which collect pollen from a few kinds of flowers (termed "oligolecty") represent a "form of host specificity" (for a review of these terms see Linsley, 1959). Yet, there has been little attempted transfer of methodologies from related studies on selective predation to the techniques used for studying selective pollination. In the following discussion, I propose an extension of a measure that I have recently developed for determining "rate of resource substitutability" among selective consumers (Covich, 1972*a*) to studies of pollinator energetics.

Before discussing these points, I want to compare plant-pollinator and prey-predator interactions. By definition, a pollinator is a dispersal agent for highly specialized pollen grains which transmit genetic information and produce sexual recombination and heterozygosity. Being direct links in the reproductive pathways of many flowering plants, pollen transporters have a strong influence on floral evolution and are tightly coupled to development of complex morphological and biochemical adaptations. Predators also have a direct effect on their prey populations, but predation (in the strict sense) can have a less intense impact if non-reproductive individuals (immature, weakened, or senescent com-

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ponents of the prey population) are eliminated. A pollinator's energetic income is derived primarily by consumption of plant products (nectar, pollen, fruit) rather than individual plants. However, a wider definition of predation has developed which makes this difference between pollinators and predators less distinct. For example, the concept of predation used in a recent review (Mooney, 1972) covers a broad spectrum of herbivorous consumption, from grazing on plant parts such as leaves and stems to "seed predation," whether the consumption eliminates a reproductive individual from the prey (*i.e.* plant) population or not. Thus, it appears that pollination fits in the broad conceptual framework of predation but also has some important special characteristics that permit pollinator-foraging to be treated as a specific subset of consumer activity. That is, pollinators are usually nectar or pollen "predators."

Since Aristotle's time, observers have noted that certain bees initially visit individual plants of one species and later shift to other species rather than flying randomly to several different kinds of flowers (Proctor & Yeo, 1972). This selective feeding behavior is often termed "flower constancy" by pollination ecologists, but their measurements and definitions of constancy are quite varied. For example, two frequently used approaches for determining degree of constancy are: i) the following of individual insects (marked with dye or radioactive tracers) as they move from plant to plant and ii) the analysis of plant species visited by marking pollen or identifying pollen from particularly distinct species that comprise the pollen load gathered by an individual insect (Free, 1970). These values are usually expressed as percentages of intra- and inter-specific visits or as percentages of "pure" and "mixed" pollen loads. There is, however, a lack of uniformity among researchers in their definitions of constancy so that comparisons among different complexes of species are difficult. For instance, V. Grant (1950) reexamined some data interpreted as "mixed" loads of *Apis mellifera* and found that "every one was 95–99% pure . . ." and that "over half of the interspecific visits paid by species of bumble-bees results in pollen pellets which were at least 95% pure." Free (1970) also concluded that "determinations of pure loads is not an entirely satisfactory way of expressing constancy . . ." A comprehensive review is presented by Faegri and Pijl (1971), who point out there has been some confusion between the terms "constancy" and "monotropy." They note that "both of them have been called 'flower constancy,' but they are entirely unrelated. A monotropic animal is (physiologically, physically, and/or ethologically) unable to utilize any other plant species Constancy is an *individual* quality in a polytropic (theoretically also in an oligotropic) animal which as a species is . . . able to, and does visit any of a number of plant species One might define constancy as an individual and (as the case may be), a temporary, monotropy in a polytropic species." They also stress the importance of perspective in defining constancy and delineate three distinct viewpoints: i) that of the flower, ii) the species of the animal pollinator, and iii) the individual visitor in relation to changes during its life history or a particular activity.

Many parallel difficulties are also encountered by ecologists dealing with

selective predation in which marked predators are visually tracked or their stomach contents and fecal pellets are analyzed. For example, the uncertainty regarding the establishment of specific "search images" by selective predators (for reviews see: Dawkins, 1971; Royama, 1970) is similar to that encountered in operationally defining "flower constancy." The major sources of difficulty in measuring feeding selectivity in these types of research are: i) reliance on percentage values rather than fully expressed ratios or other types of relative and absolute index values, ii) inadequate definitions of "resources" and "availability" so that the result is often an absence of essential information on availability of consumed resources relative to other types of foods which were present but not consumed, iii) lack of uniform time spans over which initial data are collected and general failure to incorporate temporal variables, iv) assumed uniformity for qualitative and quantitative nutritional values among the alternative energy courses, and v) lack of information on previous feeding (*i.e.* hunger levels and conditioning effects).

These problems have been recognized by other researchers and are dealt with in a variety of ways by pollination ecologists. One example is a study by Synge (1947), who used pollen traps to study foraging by colonies of *A. mellifera* relative to changing availabilities of different flowers on an hourly and seasonal basis. She designed some feeding-choice experiments but was unable to account completely for observed differences in pollen collecting between different bee colonies and notes that "it would be interesting to offer them pollens that, though plentiful, they do not appear to use to any extent, such as those from *Tilia* and the Gramineae." I have not found any reference to further experimental work in which pollen resources have been identified and tested for their relative substitutability, but Gilbert (1972), using time-lapse videotape recording, reports some important data on feeding rates and preferences by *Heliconius* for pollen and pollen-sized glass beads relative to sucrose solutions. Another approach to defining resources has focused on the biochemical characteristics of nectar resources and exploitation by specific pollinators (*e.g.* Baker & Baker, 1973; Free, 1970; Percival, 1961). Other studies have considered the energetics of nectar exploitation and emphasized the importance of relative efficiencies among pollinators in determining flower constancy (*e.g.* Heinrich & Raven, 1972; Wolf, Hainsworth & Stiles, 1972). Energy expenditures by pollinators appear to be greatly affected by proximity of resources within a three-dimensional distribution (Heinrich, 1972; Levin & Kerster, 1973). A few ecologists have stressed the necessity to search for possibly unique foraging patterns and to consider the effects of varying abundances of alternative potential resources other than nectars (and for some species, direct consumption of pollen) which may require unusual definitions of floral resources. For example, Wickler (1968) points out, "Some plants, such as *Cassia* species, have even developed special nutritive sterile pollen in addition to the normal form Other flowers, those of orchids in particular, are equipped with protein-rich edible hairs or other edible tissues" These examples of distinct viewpoints for considering precise relationships among pollinators and nutrient resources provide a good basis for avoiding the difficulties

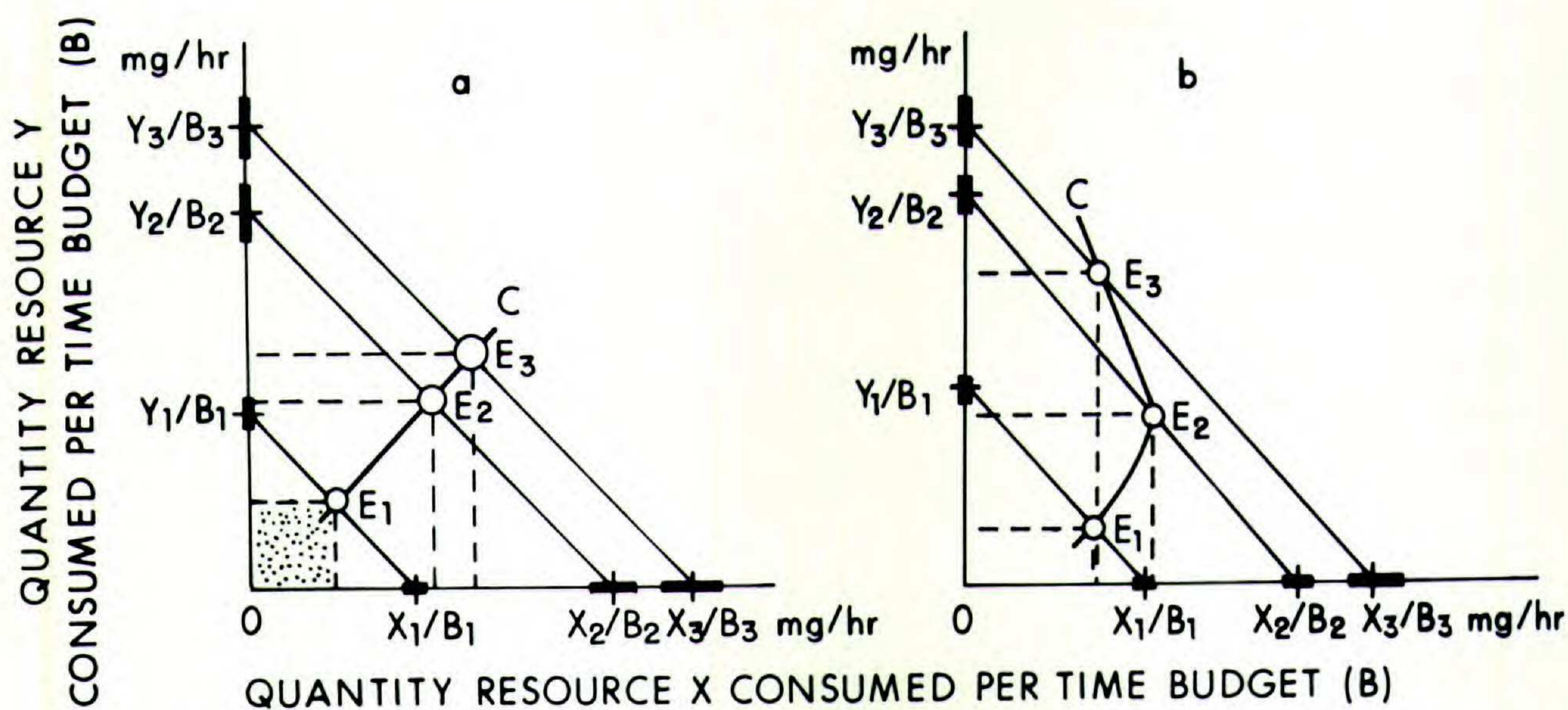


FIGURE 1. Results of hypothetical increases in feeding periods ($B_3 > B_2 > B_1$) when both resources (X, Y) are available at constant levels.—a. If equal proportions of X and Y are consumed per time budget, the resources are defined as “perfect substitutes” and the “consumption curve” (C) is positively sloped.—b. If changing proportions of X and Y are consumed per time budget so that X is preferred during short feeding periods (B_1) and Y is preferred during long feeding periods (B_3), the resources are “imperfect substitutes.” The consumption curve (C) changes from positively to negatively sloped.

involved in defining “constancy,” but additional techniques may supplement these approaches.

A wide spectrum of foraging “strategies” are reported in the ecological literature on selective predation (for reviews see: Royama, 1971; Schoener, 1971). Some of these concepts and related methodologies (particularly the “electivity” index of Ivlev, 1961) may be applicable to pollinator selectivity. The approach I propose is to define different classes of pollen and nectar resources and to measure their substitutability under varied sets of absolute and relative availabilities. The method is based on measurements of consumption rates in a series of one- and two-choice tests performed first in controlled laboratory conditions and then in manipulations of natural field populations. The consumer (*i.e.* the pollinator) is initially introduced to two potentially different types of food (*e.g.* equally concentrated nectars produced by two closely related species) which are readily available *ad libitum* and the quantities (volume, weight, or caloric content) of each that are consumed per unit time are recorded and graphed (*e.g.* Fig. 1a) on rectangular coordinates. The axes are scales of the quantities consumed of each of the different resources (X and Y) during a controlled feeding period termed the “time budget.” The limits of resource exploitation by a particular consumer within any given series of time budgets can be observed experimentally. These limits are bounded by the “time budget line.” The shape of this line is first defined by three points, one of which (Fig. 1a, E_1) is obtained by systematically repeating a series of two-choice tests of the consumer’s selection of X + Y combinations so that an average combination (*e.g.* $E_1 = 4$ mg X/hr + 4 mg Y/hr) and the variance can be calculated for a given level of abundance and time budget. The variance is represented graphically by the diameter of

the circle around each average equilibril value. The other two points that define the time budget line are determined by a series of replicated one-choice tests in which the same time budget is expended in consuming first one food (X_1/B_1) and then the other (Y_1/B_1). These average maximal intercepts on the abscissa and ordinate, together with E_1 (the average total consumption of $\frac{X + Y}{B_1}$) denote the limits of the time budget line for a particular consumer given a specific level of abundances. Thus, during the time budget B_1 a consumer can select from any range of combinations from all $Y_1 + \text{no } X_1$ to all $X_1 + \text{no } Y_1$. The relative consumer preference is indicated by the ratio of $Y_1:X_1$. That is, if the E_1 combination has equal amounts of Y_1 and X_1 (and the ratio is therefore 1:1), then the consumer has equal preference for both resources at that level of food abundance and time (as in Fig. 1a). The area in the quadrant (or "resource space") selected for consumption is represented by the stippled square in Figure 1a. Note that it is possible for the consumer to select any combination within the restraints of the time budget (*i.e.* the triangular area bounded by $Y_1/B_1 - X_1/B_1 - 0$). The portion selected indicates the consumer's evaluation of the two resources. The slope of the time budget line is the rate of substitution of Y for X, *i.e.* to select more of Y some X must be given up (or "traded off"). A more detailed discussion of these relationships and the use of this method to define specific resources (either as "perfect" or "imperfect" substitutes, or as complements) is presented in another study (Covich, 1972a).

Two types of tests are required to complete the analysis. One is to run a series of consumption measurements using the same foods and abundances but increasing the time budgets (Figs. 1a and 1b). The other is a series in which the time budget is held constant (Figs. 2a and 2b), but the abundance of one food (or the other) is changed (either by changing absolute abundance, or relative distances between units of each food, or concentration of the food such as diluting one or the other nectars). Both of these types of experiments measure the consumer's response to changes in relative resource availability and yield sets of Y_n/B_n and X_n/B_n intercepts as well as E_n values. Thus, any point in "resource space" represents a possible equilibril or mean combination of $X + Y$. Some combinations will be within and others outside the time-budgetary restraints for a particular consumer foraging on specific sets of available combinations. The series of points (Figs. 1 and 2: E_1, E_2, E_3) representing average consumption of $X + Y$ combinations per time budget is connected by a line termed the "consumption curve" (C in Figs. 1 and 2).

Inasmuch as these two distinct types of changes (*i.e.* either length of time budgets or abundances of one alternative resource) are interrelated, their separate analysis is useful because patterns of feeding behavior may shift in distinct modes and are documented independently by shapes of the C curves. For example, if the total amount of time available for feeding increases and the consumer is not saturated differently by the two foods, then the expected C curve would have a continuously positive slope (Fig. 1a: C). If the resources are exploited in a consistent manner following an increased abundance of X, the slope

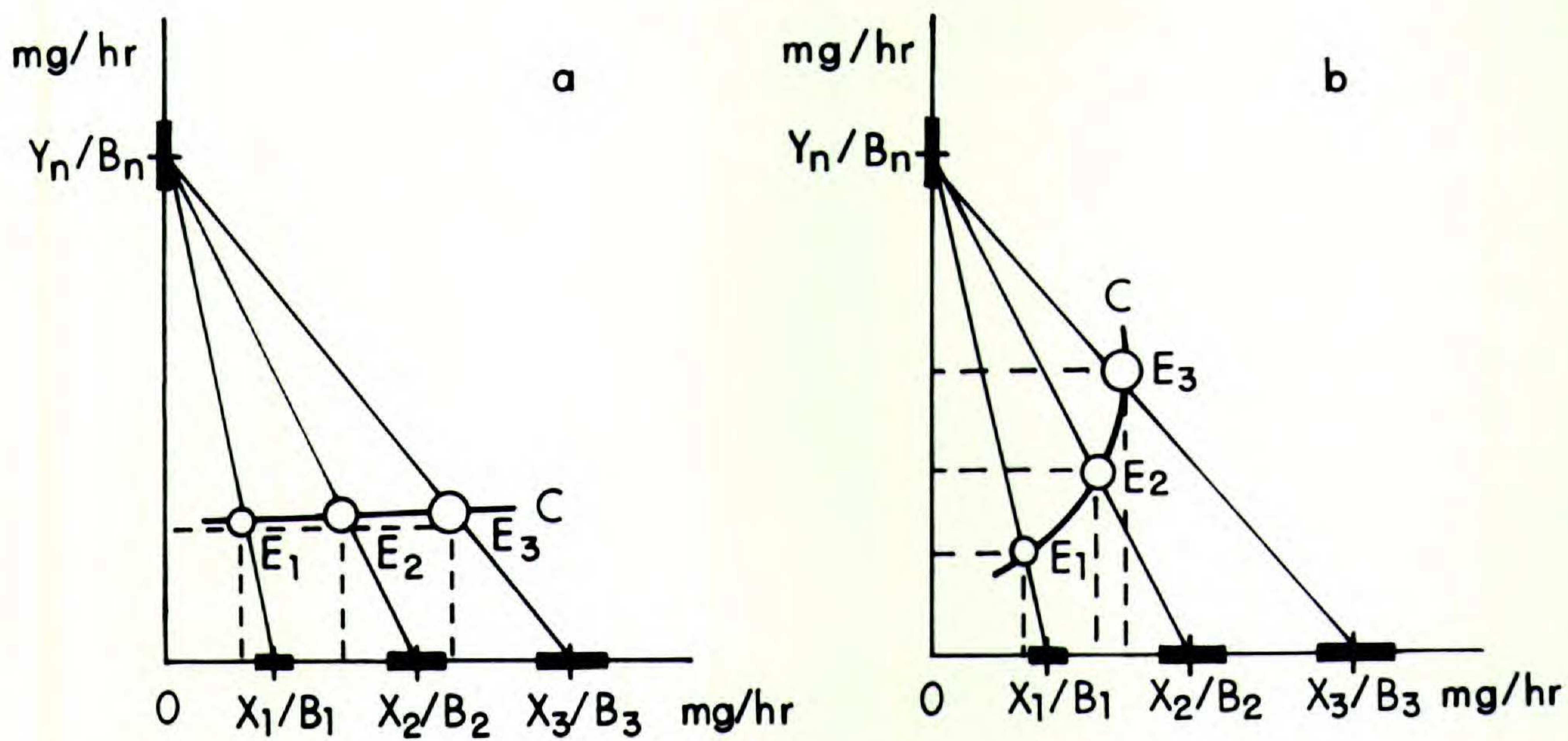


FIGURE 2. Results of hypothetical increases in availability of one resource ($X_3 > X_2 > X_1$) when the availability of an alternative resource remains constant ($Y_1 = Y_2 = Y_3 = Y_n$) and the feeding periods remain constant ($B_1 = B_2 = B_3 = B_n$).—a. If equal amounts of Y are consumed as increasing amounts of X are eaten, the two resources are defined as “poor substitutes” and the consumption curve (C) has zero slope.—b. If increased amounts of both Y and X are consumed as the availability of X increases, the two resources are defined as “complementary” and the consumption curve is positively sloped. Change in proportional consumption of Y and X indicates Y is preferred to X. These shifts in ratios of Y:X illustrate the definition of “subsidiary” resources and the concept of “time transfers.”

of C will be zero and C will be a straight line horizontal to the X axis (Fig. 2a). Rapid saturation with resource X is depicted in Figure 1b (C) following an extended time budget and in Figure 2b (C) following an increased abundance of X. One important point is that a consumer may actually eat less of one resource following an increased time budget than when that resource was relatively hard to find during a short time budget (Fig. 1b, *cf.* X:Y in E₂ and E₃). This type of shift occurs, then, if the resources are “imperfect substitutes” (*i.e.* in Fig. 1b Y is strongly preferred to X during long feeding periods). Shifts in substitutability and degree of selectivity are known to occur as consumers become satiated at high levels of abundance or if their time budgets are long (*i.e.* low restriction on searching). Increased selectivity has been clearly observed in studies on consumption isoclines of silkworms (Ishikawa *et al.*, 1969), fish (Ivlev, 1961), and mice (Covich, in preparation; Holling, 1959). Alternative models of this effect are presented by Emlen (1968), Holling (1966), Marten (1973), and Rapport (1971) and reviewed by Pulliam (1974).

The most interesting relationship occurs among selective consumers with a strong preference for one resource when the strongly preferred resource has very low availability relative to a nonpreferred (but nutritionally adequate) food resource. This non-preferred food is termed a “subsidiary” resource because the consumer can exploit it and simultaneously continue to search for the rarer, more preferred “primary” resource. If the subsidiary resource increases to extremely high levels of abundance (as depicted in Fig. 2b: $X_3 > X_2 > X_1$), the “time cost” for finding and consuming this readily available resource (X) de-

clines. Even if the time budget remains uniform (*i.e.* Fig. 2b: $B_1 = B_2 = B_3 = B_n$), more of X can be obtained with less time expended per unit X consumed (*i.e.* in Fig. 2b: $X_1/B_1 > X_2/B_2 > X_3/B_3$). The significant effect is that simultaneously more of the preferred resource (Y) can be obtained as a result of the consumer's ability to transfer time saved in searching for X to increased searching for Y. Therefore, even though the availability of the preferred primary resource remains at a constant low level (Fig. 2b: $Y_1/B_1 = Y_2/B_2 = Y_3/B_3 = Y_n/B_n$) and the time budget is constant, more of the primary resource (Y) can be included in equilibrial combinations (*cf.* E_1 to E_2 and E_3 in Fig. 2b). The proportion of Y:X in the combination shifts in response to increases in availability of the subsidiary resource (X). My current research focuses on this relationship, and I am investigating what degree of preference for primary resources and what level of abundance among subsidiary resources are necessary in order to predict complete elimination (on a local scale) of the primary resource.

Although these studies on selective consumption have focused on non-pollinators, components of some of these methods appear applicable to investigating pollinator selectivity. A generalized approach to measuring resource substitutability may help answer some questions which I feel have been generated by papers presented in this symposium. In the first paper, for instance, Heithaus proposes that we "refine our analysis to distinguish the truly potential pollinators among nectar and pollen consumers." He defines floral resources by observing which plants are in flower during a particular time, and his approach yields excellent results. The additional measurement of resource substitutability would provide another method for identifying resources independent of taxonomic relationships (*e.g.* unrelated species may produce nectars which are "perfect substitutes," or identical "resources," for some pollinators but perhaps because of differences in floral color, scent, or morphology, these resources may or may not be available to other pollinators). This supplemental information would be useful for interpreting some of his observations on foraging by butterflies in Costa Rica. For example, certain butterflies (*Anartia fatima*) have a uniform supply of nectar resources from milkweeds (*Asclepias*) throughout the year and switch to *Licania* during its brief peak abundance. It would be interesting to know if *Licania* nectar is strongly preferred to that produced by *Asclepias*. Also of importance would be the relative preference for *Cupania* and *Melanthera*, which are similarly seasonally available but not exploited by *Anartia*.

Beattie's study of *Viola* uses several methods for documenting the breadth of taxonomic diversity among pollinators. He is able to demonstrate that behavioral differences among pollen and nectar consumers determine which insects are significant pollinators. Apparently, the number of visits by pollinators may be misleading with regard to determining which species actually cross-fertilize the plants. Beattie stresses that data must be carefully obtained to distinguish differences between common species which consume resources but have little effect on the plant's productive potential, and relatively rare species whose consumption of resources may be slight but whose role in pollination is significant.

Beattie has previously considered related questions in his discussion of some

analogies between pollinators and flower-predators. Beattie, Breedlove and Ehrlich (1973) note that, "Success at avoidance of insect predators . . . would appear to militate against the evolution of specialized insect pollinators. Both specialized predators and pollinators have many problems in common, particularly synchronizing with the food source . . ." The evolution of specific synchrony between pollinators and avoidance of large population build-ups of predatory insects may be a common strategy based on supplying distinctly different ("poorly substitutable") resources to these two very different groups of consumers in distinct temporal modes of availability.

Rates of substitution may also be useful information for interpreting some of the plant-insect relationships discussed by Strong. He contends that the extension of an insect's host range (*i.e.* the "host transference" by stenophagous consumers) "is rather a common event that classical entomological methods rarely detect." That some highly selective insect consumers can rapidly shift among a restricted range of alternative food plants is well documented, but the frequency with which this switching occurs in nature is not well known. It would be impossible to document precisely the feeding behavior of numerous insects, but based on the data presented by Strong and Southwood, a few characteristics as well as exceptional species could be tested for the rate of substitutability. For example, the single species of Lepidoptera that is associated with native yews (*Taxus baccata* L.), or the one lepidopteran species currently associated with acacia (*Robinia pseudoacacia* L., introduced more than 300 years ago), might be interesting consumers to compare with regard to feeding selectivity. As Southwood (1973) suggests, the mechanism (or "degree of predilection") limiting the number of insect consumers of yew is probably a structural or biochemical one (such as phytoecdysone or the alkaloid "taxine"). The significance of these exceptions to the general relationships between numbers of insects and tree abundances may be considerable. But in addition to these exceptional instances of coadaptations, there is a more general set of interspecific competitive interactions among insects colonizing and exploiting plant resources. Some of these complex relationships occur over varied ecological and evolutionary time scales which may limit the usefulness of isolated studies of feeding selectivity. As Janzen (1973) points out, "All the parts of an individual plant are connected through the medium of its resource budget. Since this budget is subject to selection at the level of the individual plant, a species of insect colonizing it over evolutionary time will automatically compete with *all* other species of insect already established on the island (plant)."

In contrast to the breadth of the plant-animal associations discussed by Heithaus, Beattie, and Strong, the reciprocity among figs and fig wasps of the family Agaonidae is characterized by extremely narrow specialization. Ramírez presents a detailed account of these complex coadaptations which illustrate the limits on obligate mutualists. Neither the flowers nor the pollinators can reproduce without the other, and nearly each species of *Ficus* is pollinated by a distinct chalcidoid wasp (even the highly specific pollinating wasps serve as hosts to other species of wasps which are specialized to parasitize them). The

inability of these chalcidoid wasps to switch to alternative fig flowers limits the reproductive distributional patterns of both these groups. Ramírez (1970) presents a possible link between dispersal of *Ficus* and fruit-eating bats. Not only is there a strong correlation between the distributions of figs and these bats, but Ramírez observes that bats do occasionally transport both the mature fig fruits and the wasps which are entrapped.

Ayensu presents an interesting case study in selective feeding by bats which illustrates some important general principles regarding resource definition. He notes that the neem tree (*Azadirachta indica*) was introduced to West Africa some 60 years ago without any idea of the rapidity at which it might spread and displace the indigenous vegetation. The seeds are dispersed by fruit eating bats (*Epomophorus gambianus*) which have become extremely numerous. Inability to predict these trophic dynamics probably occurred because the flexibility of bat feeding behavior was not understood. Perhaps more important, however, is the complexity of bat feeding which would have hindered the predictability of even a very good methodology for measuring resource substitution by bats. Ayensu notes that "although neem fruits are available on the tree on which bats roost, they are not eaten Similarly, the *Eidolon helvum* that roost in the palms in Ghana do not feed on the fruits of the same tree, but fly to another palm to feed." These are remarkable illustrations of the difficulties of defining resources and in measuring their absolute availabilities, and similar examples exist for other highly mobile consumers (*e.g.* Brown, 1969). Identification of food resources generally requires study of both temporal and spatial variables in a framework that incorporates distinct and rapid changes in consumer behavior.

The phenological classification proposed by Gentry relates directly to the general problem of food resource availability. As he points out, there are distinct types of blooming periodicity in Bignoniaceae, all of which require some expenditures of energy by plants in order to produce nectar and pollen for attracting pollinators. Of particular interest are the relationships between some of these distinct types of periodicity. Certain species (Gentry's "type 5") synchronize short periods of flower production and develop numerous blossoms that lack nectar. These flowers still attract sufficient insect pollinators from other species (types 1, 2, and 3), especially from those characterized by more prolonged production of large masses of flowers containing abundant nectar (type 4). Gentry proposes that the species lacking nectar are "mimics" of nectar-producing mass flowering species. The dynamics of this interesting hypothesis could be experimentally tested by manipulating the availabilities (*i.e.* flower frequency and spacing or nectar concentration) of co-occurring "model" species which produce the nectar. Pollinators have different energetic demands and conditioning thresholds which could be compared in terms of their effects on fertilization and seed production among both models and mimics. Field manipulations could be designed to answer questions such as: i) What is the lowest possible nectar availability (in type 4 flowers) which would allow a specific pollinator sufficient time and energy to search for other sources of nectar (some

being type 5 flowers without nectar)? ii) Do pollinators learn to substitute markedly different nectar resources (or migrate to habitats with different flowers) if the proportion of type 4 to type 5 flowers is below their energetic demands?

The general significance of various types of "mimicry" is further discussed by Macior, who offers additional examples. His documentation of pollinator behavior with slow motion films is an effective method for recording actual expenditures within the limits of a given pollinator's time budget. As a result of his detailed studies, it is readily apparent that flower constancy (and resource substitutability) are relative measures in need of a high degree of precision.

Several other pollination ecologists (*e.g.* K. A. Grant, 1966; Yeo, 1968) have interpreted aspects of convergent floral evolution which relate directly to these reports by Gentry and Macior. For example, Grant (1966) notes that "the existence of common red coloration is of evolutionary significance in providing an instance of a situation in plants comparable to the phenomenon of Mullerian mimicry among animal species." Proctor and Yeo (1972) discuss several cases of floral evolution they consider to be "the result of *Mullerian mimicry*—in which a number of species of similar character and behavior, and of comparable abundance, have evolved a common 'advertising style' to their mutual advantage . . ." and others that "are examples of *Batesian mimicry*, in which one organism obtains a one-sided advantage by imitating another organism more numerous than itself." This latter extension of the concepts of Batesian and Mullerian mimicry to include plant-pollinator interactions may cause some ecologists to object on the grounds that animals with aposematic coloration provide a signal to *repel* their predators (models typically are toxic or distasteful to specific consumers who learn to avoid them), whereas flowers evolve signals to *attract* their pollinators. Clearly, the consumers learn by distinct modes either primarily through negative reinforcement (for distasteful prey) among predators or through positive reinforcement (for nectar rewards) among pollinators. Yet, these two different types of evolutionary processes do have important linkages between them. For example, in regard to evolution of red coloration in both faunal prey and flowers, Cott (1940) notes, "The efficient reception of red light by the eye of diurnal birds is linked up with extensive use, by utterly unlike organisms and structures, of orange, vermilion, crimson, and scarlet, in typical bird-advertisements: and this, although their functions may be diametrically opposed—in the one case being attractive, in the form of flowers or fruit; in the other repellent, in the shape of dangerous or distasteful prey." Both among faunal Mullerian mimics and among convergently evolved red-colored flowers there is increased efficiency in learning by the associated consumers (predators or pollinators) as the number of species and individuals with the same coloration (or "signal") increases in abundance. Furthermore, as Raven (1972) suggests, these coevolving species are complexly integrated in terms of their energetic budgets so that the probability of outcrossing is maximized.

In the concluding discussion of the symposium, Dodson stated he felt evolution of floral coloration was sufficiently different from warning coloration in Batesian and Mullerian mimics to preclude extending these concepts to include

convergence of flower color. He noted the general phenomenon of "deception" covers a wide range of specializations from "pseudo-copulation" among orchid flowers and male pollinators to common patterns of red-orange coloration in groups such as *Asclepias* and *Lantana*. For sake of definitional clarity, it may be necessary to consider some of these forms of deception as instances of "aggressive mimicry" (also termed "Peckhamian mimicry") to differentiate them from other distinct types of mimicry as Wickler (1968) suggests. The analogy between Batesian mimicry in animals and plants can, however, be useful in suggesting parallels for experimentally testing putative floral relationships. The significance of balanced proportions among model and mimics is now well documented (*i.e.* the consumer learns to recognize the palatable mimic very quickly if it is brightly colored and if there are relatively few distasteful models to frequently reinforce the relationships between the bright pattern of coloration and toxicity). I have previously suggested (Covich, 1972*b*) that non-toxic varieties of *Manihot esculenta* may be subject to less attack by herbivores when interplanted among toxic varieties containing cyanogenic glucosides. I am currently investigating these relationships in Mayan "milpas" where both toxic and non-toxic varieties of manioc are simultaneously cultivated. Model-mimic relationships have been tested among several species in ways (as reviewed by Brower, 1970; Rothschild, 1973) which may be partially applicable to laboratory and field experiments on floral nectar exploitation.

The participants in this symposium present a broad range of studies dealing with a diverse array of coevolving plants and animals. The large number of different methodological approaches reflect the heterogeneous nature of these multispecific interactions and the widely different questions being asked. Despite these distinctly varied interactions, some questions regarding selective herbivory and pollination can be broadly compared. To characterize some questions which need solutions, I review the concept of flower constancy and discuss some analogies with other concepts such as specific searching image, Batesian mimicry, and the analysis of consumer choice as measured by rate of resource substitution. These analogies do provide some interesting hypotheses, but testing them will require innovative field methods. Their successful development and application can be expected to yield considerable insight into population dynamics and the regulation of coevolving communities.

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